Effects of predation on temporary autumn populations of subadult *Clethrionomys glareolus* in forest clearings

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Abstract

Using netting to exclude both avian and mammalian predators in a field experiment we investigated the effect of predation and predation risk on survival, body weight development and microhabitat preferences of temporary, subadult *Clethrionomys glareolus* populations in two forest clearings during the autumn of 1996. Female bank voles were found to be influenced to a higher degree than males. Female survival was higher on predator-excluded grids compared to predated grids, whereas there was no clear response in males. Females also gained more weight on predator-excluded grids compared to both males on the same grids and females on predated grids. There was no clear treatment effect when mean body weights were compared in each trapping period. However, mean female body weights on predator-excluded grids were significantly higher in November than in September. This was not the case on predated grids.

There was a clear treatment effect on female microhabitat preferences. On predated grids female bank voles were captured at trap stations with more cover than females on net grids. A similar but less clear tendency was seen in males. On both net grids in both September and November female bank voles were trapped at trap stations with less cover than males, whereas the opposite was true for both predated grids in both months.

Key words: *Clethrionomys glareolus*, survival, predation risk, microhabitat preference

Introduction

Since slightly more than the last decade attention in studies of predation on small rodents has been increasingly directed towards the indirect effects on the prey animals. Apart from the more direct effects on survival, recent studies have dealt with effects on activity, reproduction, foraging behaviour, spatial distribution, microhabitat selection, and body weight (Abramsky et al. 1996; Hendrie et al. 1998; Holmes 1991; Jedrzejewska and Jedrzejewski 1990; Jedrzejewski et al. 1993; Koivunen et al. 1998; Koskela et al. 1996; Lagos et al. 1995; Otter 1994; Ylönen and Ronkainen 1994; Yoccoz and Mesnager 1998).

Bank voles (*Clethrionomys glareolus*) have been shown to suppress reproduction in the laboratory in response to odours from small mustelids and in the field in response to actual predation (Ylönen 1989; Heikkilä et al. 1993; Korpimäki et al. 1994; Ylönen and Ronkainen 1994; Mappes and Ylönen 1997). Recently, however, the laboratory results have been questioned (Mappes et al. 1998). In seminatural enclosure experiments intra-specific aggressiveness in the bank voles decreased in response to predation risk (Jedrze-

JEWSKA and JEDRZEJEWSKI 1990). Bank voles have also been shown to respond to perceived predation risk by decreasing other activities, e. g. foraging activity (JEDRZEJEWSKI et al. 1993; YLÖNEN and RONKAINEN 1994). This decreased foraging activity has been suggested as the cause of the decreased body weights found in predator-exposed bank voles in some laboratory studies (YLÖNEN 1989; YLÖNEN and RONKAINEN 1994; KOSKELA and YLÖNEN 1995). Other studies have found no effects on body weights under laboratory conditions (KOSKELA et al. 1996; MAPPES et al. 1998). In the field a few studies on bank voles also point at a negative effect of predation on body weight (MARTINSSON et al. 1993; YOCCOZ and MESNAGER 1998) but other researchers found no effects (MAPPES et al. 1998).

Accordingly, the influence of predation on body weight in bank voles is still debated while field studies on the issue are scant. Body weight may affect social status, survival, and reproductive output (STENSETH et al. 1977; COLE and BATZLI 1978; IMS 1987; PUCEK et al. 1993; CARLSEN et al. 1999) and therefore we regard the question of the influence of predation on body weight as rather important. The aim of the present short-term field study was to investigate effects of predation on survival, individual body weight, and microhabitat preferences in a population of subadult *Clethrionomys glareolus*.

Material and methods

The field tests were carried out in two large clearings, planted with young beech or oak trees in a forest near (< 40 km) Copenhagen, Denmark. Two sites (A and B) with all together 4 trapping grids were established. Two grids (net grids NA and NB) of 8400 and 6000 m^2 respectivly were covered with nets (mesh size 70 mm, height 2 m and fastened to the ground along the sides) to exclude predators, two grids (predator grids PA and PB) of 8100 and 7000 m^2 respectively were equipped with 4.5 m tall perches and nestboxes for kestrel *Falco tinnunculus* (Linnaeus, 1758) and tawny owl *Strix aluco* (Linnaeus, 1758).

The setup was aimed at research on field voles *Microtus agrestis*. However, 1995 was a beech and oak mast year in Denmark and the following peak year (1996) was characterized by large autumn populations of *Clethrionomys glareolus* in some forest clearings. These populations consisted mainly of subadults and disappeared almost completely during the winter 1996/97. These populations of subadult bank voles were studied with respect to the effects of predation and predation risk on survival, body weight, and microhabitat choice.

We did not obtain data to quantify the presence of predators on the grids. Predator activity estimates were mainly based on observations done during trapping sessions and – as a consequence – very rough. However, sand and snow tracking, faeces collections, and observations of dug out burrows showed that foxes *Vulpes vulpes* (Linnaeus, 1758), cats *Felis silvestris f. catus*, and least weasels *Mustela nivalis* (Linnaeus, 1766) were frequent guests on both predator grids. Occasionally, tracks or faeces from *Martes* sp. were found as well. Least weasels could pass the nets and were captured on all 4 grids, but not more often on the otherwise predator-free net-covered grids. Tawny owls *Strix aluco* (Linnaeus, 1758) and buzzards *Buteo buteo* (Linnaeus, 1758) were frequently observed and occasionally kestrels were seen hunting. On both predator grids the perches were used frequently by raptors and owls but it is not known whether this led to a more intensive predation on these grids.

Ugglan "Special" and Ugglan "Lämmel" multiple live-traps (Grahnab, Hillerstorp, Sweden) were used, one of each type at each trapping station. Traps contained wood chips for bedding and wheat for bait. There was a 10 m spacing between rows as well as between trapping stations in each row. Bank vole data from sites A and B come from trappings conducted for four consecutive nights in September and November 1996. All captured bank voles were toe clipped for individual identification. Body weight, sex, reproductive condition, trap type, and trap location were recorded for each capture. Body weight can vary with e. g. time spent in the trap or with amount of food in the digestive system. The influence of time spent in the trap was reduced by inspecting the traps on all grids at the same time of the day (between 9 and 12 a. m.) assuming that the voles by then would have spent largely the same amount of time in the traps. Furthermore weight measured on the first capture occasion of an individual in each trapping period was used to reduce the influence of weight changes caused by repeated captures within a short time.

Relative individual body weight change between two capture sessions was calculated as the difference in body weights between the two sessions divided by the body weight at the first of the two sessions. That is, for any given interval the individual weight change is calculated using the weights of individuals captured at both ends of this interval.

Return rate is the product of survival and capture probabilities and generally underestimate survival probabilities. Furthermore, differences between groups do not necessarily imply differences in survival probabilities (Lebreton et al. 1993). Despite this shortcoming return rate has the advantage that it can be used with only two trapping sessions.

At each trap station vegetation and litter cover were estimated during February and March 1997. Cover from vegetation or litter was judged at a scale from 1 (no cover) to 5 (full cover). The vast majority of the cover was constituted by perennial grasses, litter, *Epilobium angustifolium*, and *Rubus fruticosus*. The cover score on the 1 to 5 scale was therefore largely similar irrespective of time of the year.

Results

The return rate was 46–75% for both sexes at all grids between September and November (Tab. 1). At both net grids females had higher return rates than the females on the neighbouring predator grids. Males at net grid A had lower return rate than males at predator grid A, whereas males at net grid B had higher return rates than males at predator grid B. None of these differences, however, were significant (Tab. 1).

At both site A and B females on the net grids gained weight between September and November (Tab. 2). At site A males on the net grid and both sexes on the predator grid lost weight. At site B the weight gain of net grid males and both males and females on the predator grid was less than the weight gain of net grid females. None of the differences were significant (Tab. 2). However, the pattern of the individual weight changes was almost identical at the two sites. Individual weight changes of net grid males and predator grid females and males were all similar at each site, and the difference between net grid females and net grid males or between net grid females and predator grid females were very similar (Tab. 2).

We found no significant differences in mean body weights between the sexes on any grids in any month. In September female bank voles on predator grid A had a significantly higher mean body weight than females on net grid A (Tab. 3). Apart from that no significant differences between grids were found. On both net grids, however, the mean body weight of females was significantly higher in November than in September (Tab. 3). Also males on predator grid B weighed significantly more in November than in September. No other significant differences in mean body weights between trapping periods were found. As immigrants (newly marked individuals) in November 1996 constituted only 11–19% of the bank vole populations at sites A and B we consider changes in mean weights mainly a result of individual weight changes.

Females on predator grids were trapped at trap stations with significantly more cover than females on net grids (Tab. 4). Duncan's mutiple range tests shows a clear treatment

Table 1. Return rate of female and male bank voles between September and November 1996 on the two net grids (NA and NB) and two predator grids (PA and PB). Results of chi-square test are shown.

Sex	Site	Net grid	Predator grid	Chi-square	P
Female	A	0.714	0.556	1.06	0.303
	B	0.688	0.481	1.73	0.189
Male	A	0.500	0.750	3.05	0.081
	B	0.667	0.462	2.08	0.149

Table 2. Mean individual weight change/g body weight for bank voles between September and November 1996 on the two net grids (NA and NB) and two predator grids (PA and PB) with 95% confidence intervals. Results of all effects ANOVA and Duncan's multiple range test are shown.

| Site A | All Effects: F = 1.605, P = 0.201 | | | P-values of each pair | | |
| | | | | NA | | PA |
Grid	Sex	N	Mean individual weight change/g	Females	Males	Females
NA	Females	14	0.060 ± 0.089			
	Males	13	−0.021 ± 0.041	0.118		
PA	Females	9	−0.018 ± 0.085	0.111	0.954	
	Males	14	−0.025 ± 0.069	0.115	0.941	0.902
Site B	All Effects: F = 1.252, P = 0.301			P-values of each pair		
				NB		PB
Grid	Sex	N	Mean individual weight change/g	Females	Males	Females
NB	Females	11	0.149 ± 0.094			
	Males	12	0.057 ± 0.106	0.126		
PB	Females	13	0.049 ± 0.085	0.109	0.891	
	Males	18	0.061 ± 0.063	0.120	0.949	0.852

effect in both September and November where the mean cover index value for female bank vole captures were significantly higher on both net grids compared to any of the predator grids. The males too showed a tendency for captures under denser cover on the predator grids but the pattern is not as obvious as for the females (Tab. 4). The clear pattern in the females compared to the males resulted in females being captured at trap stations with denser cover than males on the predator grids, whereas they were captured at stations with less cover on the net grids (Fig. 1). The difference between the sexes was only significant on predator grid B in September where females captures were under denser cover than male captures. However, the described difference between net and predator grids were consistent on all grids in both trapping periods.

Discussion

In laboratory and semi-natural experiments higher weight losses in voles exposed to predator odours compared to control voles have been frequently found (YLÖNEN 1989; YLÖNEN and RONKAINEN 1994; KOSKELA and YLÖNEN 1995; MAPPES and YLÖNEN 1997; CARLSEN et al. 1999) although some researchers did not find any effect of predator odour (KOSKELA et al. 1996; MAPPES et al. 1998).

In the field several studies have found rodent foraging behaviour to be influenced by predation risk (OTTER 1994; ABRAMSKY et al. 1997). Common for these field studies is the fact that the rodents did not necessarily reduce foraging activity but rather redistributed it to include a larger proportion of relatively safe areas. However, researchers have suggested that predation does have an effect on body weights in the field. MARTINSSON et al. (1993) found higher body weights in a bank vole population on a predator-free island compared to a mainland population. YOCCOZ and MESNAGER (1998) found higher body

Table 3. Mean weights of female and male bank voles on the two net grids (NA and NB) and two predator grids (PA and PB) with 95% confidence intervalls. t-test results for the comparisons between grids at each site and for the comparisons between months for each sex are shown.

Females				Site A	Comparison between months	
		September		November		
	N	Mean weight	N	Mean weight	t	P
Net	23	16.0 ± 1.0	20	17.5 ± 1.2	2.072	0.045
Predator	19	17.5 ± 1.1	21	17.4 ± 1.0	0.136	0.893
t		2.266		0.029		
P		0.029		0.977		

Males				Site A	Comparison between months	
		September		November		
	N	Mean weight	N	Mean weight	t	P
Net	31	16.2 ± 0.6	19	16.7 ± 1.2	0.853	0.398
Predator	19	17.0 ± 1.2	19	16.2 ± 0.8	1.237	0.224
t		1.310		0.836		
P		0.196		0.410		

Females				Site B	Comparison between months	
		September		November		
	N	Mean weight	N	Mean weight	t	P
Net	20	16.7 ± 0.8	12	19.1 ± 1.4	3.427	0.002
Predator	31	17.5 ± 1.0	15	18.3 ± 0.8	1.043	0.303
t		1.211		1.165		
P		0.232		0.255		

Males				Site B	Comparison between months	
		September		November		
	N	Mean weight	N	Mean weight	t	P
Net	23	17.6 ± 0.9	16	18.6 ± 0.9	1.544	0.131
Predator	46	17.0 ± 0.5	21	18.9 ± 1.2	3.361	0.001
t		1.100		0.398		
P		0.275		0.693		

weights in alpine bank voles compared to lowland populations and suggested that lower impact of predation was the cause. We have previously shown negative influence of predation risk on *Microtus agrestis* body weights in the field as well as in the laboratory (Carlsen et al. 1999).

The present study shows larger individual weight increase in female bank voles in autumn in predator-excluded populations compared to predated populations. Males, on the other hand, did not respond so clearly to predator exclusion. As immigrants only made up a small proportion of the November population the individual weight increases in net grid females influenced mean body weights so that female November weights on net grids were significantly higher than female September weights on these grids. However, we found significant differences in mean body weight between treatments only in one case in September. This stresses that possible effects of predation on body weight in the field may be better shown by comparisons of individual body weight changes and mean weight differences over time than by comparing differences in mean weight between treatments (Carlsen et al. 1999).

Also regarding survival and microhabitat preferences females responded more clearly to predator exclusion than males. Female survival was higher on both net grids whereas male survival did not show clear treatment effects. This is in accordance with results on *Microtus agrestis* indicating female survival to be more affected by predator exclusion

Table 4. Mean cover index for bank vole captures with 95% confidence intervals. Results of Mann-Whitney U-test for individual comparison are shown. Also Results of Kruskal-Wallis H tests are given. N is the number of voles. Grids are not significantly different from each other share significance terms (ST).

Females

Grid	N	Mean cover index value/capture September 1996 H = 46.118, P = 0.0000	ST	U for each pair			P for each pair		
				NA	NB	PA	NA	NB	PA
NA	21	3.03 ± 0.17	c						
NB	64	3.20 ± 0.09	b	448.5			0.010		
PA	14	3.71 ± 0.15	a	23	116		0.000	0.000	
PB	35	3.53 ± 0.12	a	120	566.5	176	0.000	0.000	0.077

Grid	N	Mean cover index value/capture November 1996 H = 41.170, P = 0.0000	ST	U for each pair			P for each pair		
				NA	NB	PA	NA	NB	PA
NA	19	3.08 ± 0.23	c						
NB	20	3.00 ± 0.15	c	154			0.268		
PA	18	3.94 ± 0.19	a	24	12		0.000	0.000	
PB	18	3.39 ± 0.11	b	104	68	42	0.019	0.000	0.000

Males

Grid	N	Mean cover index value/capture September 1996 H = 12.583, P = 0.006	ST	U for each pair			P for each pair		
				NA	NB	PA	NA	NB	PA
NA	31	3.10 ± 0.18	c						
NB	64	3.33 ± 0.09	b	754			0.037		
PA	19	3.61 ± 0.26	a	157.5	405.5		0.004	0.016	
PB	58	3.22 ± 0.14	bc	772	1651	339	0.237	0.240	0.007

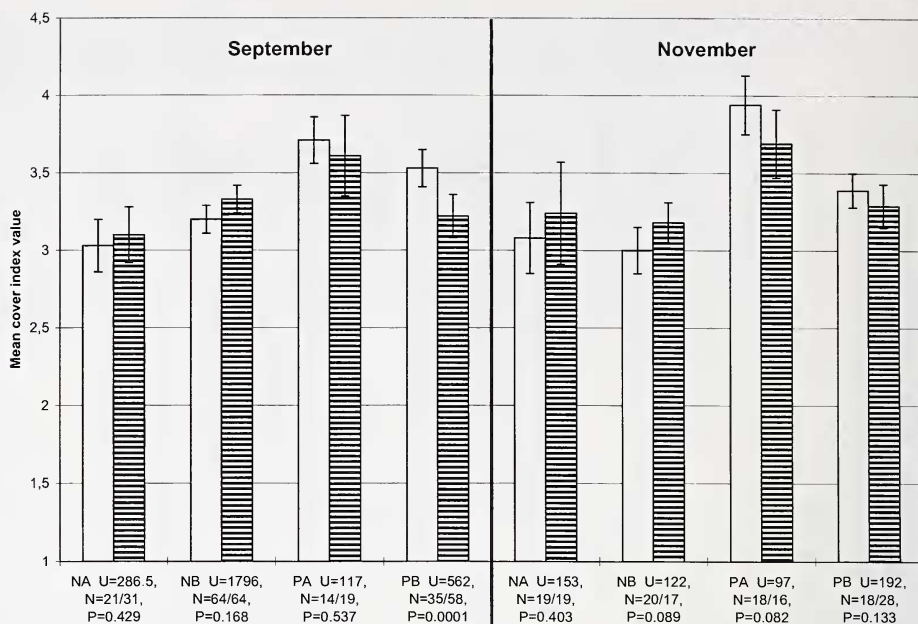| Grid	N	Mean cover index value/capture November 1996 H = 12.337, P = 0.006	ST	U for each pair			P for each pair		
				NA	NB	PA	NA	NB	PA
NA	19	3.24 ± 0.33	b						
NB	17	3.18 ± 0.13	b	146			0.599		
PA	16	3.69 ± 0.22	a	94.5	44		0.048	0.000	
PB	28	3.29 ± 0.14	b	264	208	108	0.963	0.418	0.003

Fig. 1. Mean cover index value for female (white columns) and male (barred columns) bank voles on the two net grids (NA and NB) and two predator grids (PA and PB) in September and November 1996 with 95% confidence intervals. Results of Mann-Whitney U-test are given below the columns.

than male survival both in and outside the breeding season (unpublished data). Female rodents have been found to be more susceptible to mammalian predation at least in the reproductive season (Cushing 1984; Norrdahl and Korpimäki 1998) while males are more susceptible to avian predation (Beacham 1979; Korpimäki 1985; Koivunen et al. 1996). The present results indicate that female bank voles outside the reproductive season may be under heavier influence of combined mammalian and avian predation than males.

Microhabitat choice have often been found to be influenced by predation. Pikas *Ochotona collaris* did not venture far from protective talus piles despite better food opportunities further away (Holmes 1991). The herbivorous South American rodent *Octodon degus* used spaces away from shrubs more often when predators were excluded (Lagos et al. 1995). In bank voles the use of trap sites have been found to be positively correlated with the percent cover of shrubs and tall herbaceous plants (Jensen 1984; Geuse et al. 1985; Chetnicki and Mazurkiewicz 1994; Mazurkiewicz 1994). The most important function of this shrub layer is suggested to be protection from predators (Chetnicki and Mazurkiewicz 1994; Mazurkiewicz 1994). In the present study especially females on net grids respond to the exclusion of predators by using trap sites with significantly less cover than the females on predator grids. Males showed the same tendencies but not as clearly as females. As a result the mean cover index value for females on net grids was consistently smaller than for males, whereas the opposite was true for predator grids. This is in accordance with results on *Microtus agrestis* showing a slightly increased preference for cover on predated grids compared to predator-exclusion grids (unpublished data).

The finding that female survival and female weight changes were influenced to a higher degree by predation than that of males could be a function of heavier predation pressure upon females than upon males also outside the breeding season. Experiments by

JEDRZEJEWSKA (1989), however, showed that the susceptibility of reproductively non-active bank voles to weasel predation did not differ from that of reproductively active females. Outside the breeding season females showed a more consistent clumping tendency than males which had less overlapping home ranges (KARLSSON 1986). This could make them more vulnerable to patch-seeking predators. Furthermore, it might enable the females to clump in patches with a higher degree of cover in response to increased predation risk. The males relative avoidance of each other would make them unable to respond to predation risk by increasing the use of cover to the same degree as females. Irrespective of age, males had larger home ranges than females in October (MAZURKIEWICZ 1971). A larger home range in a heterogeneous environment may also increase the chance of the male being captured at stations with less cover.

Acknowledgements

Zusammenfassung

Auswirkungen von Feinddruck auf Herbstpopulationen von subadulten Clethrionomys glareolus in Waldlichtungen

Unter Ausschluß von Prädation durch Vögel und Säuger mit Hilfe von Netzen wurden im Herbst 1996 in einem Freilandexperiment die Auswirkungen von Feinddruck auf Überlebensrate, Körpergewichtsentwicklung und Habitatwahl bei subadulten Rötelmäusen auf zwei Waldlichtungen untersucht. Weibliche Rötelmäuse zeigten dabei stärkere Effekte als männliche. In Abwesenheit von Prädatoren ergab sich gegenüber einer normalen Situation bei Weibchen eine höhere Überlebensrate, bei männlichen jedoch nicht. Weibchen zeigten auch eine stärkere Gewichtszunahme bei Ausschluß von Feinddruck verglichen mit Männchen in entsprechender Situation und gegenüber Weibchen mit Feinddruck. Unterschiede ergaben sich auch in bezug auf bevorzugte Microhabitate, denn weibliche Rötelmäuse wurden bei ausgeschlossenem Feinddruck in größerem Ausmaß in Fallen in offenem Gelände gefangen, unter Feinddruck hingegen stärker in solchen, die in der Vegetation versteckt plaziert waren. Bei Männchen zeigte sich eine ähnliche, allerdings weniger deutliche Tendenz.

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